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Sibling competition and not maternal allocation drives differential offspring feeding in a sexually size-dimorphic bird

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Sexual conflict vs maternal sex allocation in twins

Sex allocation models still fail to predict the complex sex-ratio patterns in broods of vertebrates. A major problem when studying mother-brood interactions is the difficulty to disentangle hypotheses involving maternal preferences from processes that do not imply maternal manipulation. Here we study maternal resource allocation in mixed-sex, same-sex and single-chick broods in the great bustard (*Otis tarda*). Females normally rear a single chick, and previous work has shown that maternal investment influences male breeding success more than female. Therefore, mothers of two-chick broods were assumed to be in good condition and candidates to show a preference for sons. Results showed that male chicks of mixed-sex broods remained twice as long closer to the mother than their sisters, and received double number of maternal feedings. However, sex differences in maternal feeding rate disappeared when considering only simultaneous begging approaches from both siblings. Proximity to the mother and its interaction with begging approach intensity were the factors determining the higher begging success of male chicks. In single-chick broods female chicks did not receive less maternal feedings than male chicks. Overall, our results suggest that female chicks of mixed-sex broods become outcompeted by their larger brothers, who remain much longer close to the mother, preventing sister siblings from taking a larger share of maternal feedings. We conclude that mothers do not show a preference to feed male chicks over female chicks, and that the sex differences in feeding rate are determined by the higher food requirements of male chicks due to their sexually selected, much faster growth rates. The higher mortality of female siblings in mixed-sex broods contrasts with the pattern of male-biased mortality typical in this species, and supports our interpretation of an asymmetric competitive ability of male offspring as the mechanism responsible for the sex-bias in maternal expenditure.

Keywords: differential mortality hypothesis, maternal care, *Otis tarda*, sex allocation, sexual conflict, sexual size dimorphism, sibling competition

Four decades after Fisher (1930) presented his famous theory on equal parental investment among offspring of both sexes, Trivers & Willard (1973) proposed that when resources allocated to offspring of one sex provide greater fitness returns, parents in good condition, or in years with more resources, are expected to invest more in that sex. This hypothesis was later generalized (Charnov, 1982; Frank, 1987; Leimar, 1996; Lessels, 1998), and various extensions and new hypotheses were proposed (advantaged daughter, attractiveness, local mate competition, local resource competition, repayment, cost of reproduction, male exploitation, brood reduction hypotheses; reviewed in Frank, 1990; Clutton-Brock, 1991; Hardy, 1997; Sheldon, 1998; Cockburn et al., 2002; Sheldon & West, 2004; Uller, 2006). These hypotheses raised enormous interest and numerous empirical studies have provided evidence for differential investment in sons and daughters (reviewed in Clutton-Brock et al., 1982; Gomendio et al., 1990; Clutton-Brock, 1991; Hewison & Gaillard, 1999; Cockburn et al., 2002; Cameron, 2004; Sheldon & West, 2004; Uller, 2006; West, 2009; Robert et al., 2010; Froy et al., 2016). However, in spite of such a vast literature, sex allocation theory has been very successful in predicting sex ratio adjustment in haplodiploid insects, but not in birds and mammals, where sex ratio control by parents is still poorly understood.

In birds and mammals, adjustments predicted by theoretical models often fail, probably because these models do not incorporate the complexities of their life histories (Krackow, 2002; Pen & Weissing, 2002; West & Sheldon, 2002; West et al., 2002; Uller, 2006), the difficulties of predicting sex-ratio adjustment when several offspring of the same litter compete for limited resources (Frank, 1990; Carranza, 2004), or because current models still lack an appropriate integration of theory and empirical data (Clutton-Brock, 1991; Godfray & Werren, 1996; Carranza, 2002). For example, Carranza (2004) and Uller (2006) suggested that sex asymmetries in competitive ability, cooperative behavior, and even non-competitive interactions among offspring have not been sufficiently incorporated in previous models, and concluded that investigating these interactions should increase our knowledge of sex ratio strategies in vertebrates. In addition, most authors coincide in arguing that another major problem with sex

allocation hypotheses is that their predictions are difficult to distinguish from those of evolutionary processes that do not imply maternal manipulation (Clutton-Brock, 1991; Cockburn et al., 2002; Krackow, 2002). For example, a bias in offspring sex ratio is predicted by the Trivers-Willard and cost of reproduction hypotheses, but also by the differential mortality hypothesis, since the faster growth rates and greater nutritional requirements of young males of many species (e.g. most mammals, polygynous birds) make them more vulnerable to starvation than young females (Cockburn et al., 2002). A clear indication of whether any mechanism of maternal expenditure division among sons and daughters is a consequence of active parental manipulation or of ecological constraints ultimately determined by other evolutionary forces such as, in this case, sexual selection, is only likely to be achieved by well designed experiments (see e.g. Nager et al., 1999; Merklings et al., 2015), or detailed studies of the way in which parents treat individual offspring and of the fitness consequences of sex-specific sibling interactions (Clutton-Brock, 1991; Cockburn et al., 2002; Uller, 2006).

Here we present the results of one of such detailed studies, on maternal expenditure in great bustards (*Otis tarda*). Since we were interested in investigating if mothers in good condition decide to expend more effort in her sons, we primarily studied the behavior of families with two chicks of different sex, henceforth *mixed-sex broods*. By selecting families of two chicks we ensured that mothers in our study were in better than average condition, since great bustard females usually rear one chick, and only in years with good environmental conditions experienced mothers rear two, or very exceptionally even three chicks (Morales et al., 2002; Magaña, 2007). We also studied families with two chicks of the same sex, henceforth *same-sex broods*, and families of one chick, hereafter *single-chick broods*, and used them as controls for the sex-related differences in mother-offspring, or sibling interactions observed in mixed-sex broods. In two-chick broods, based on observations of the behaviour of mother and both offspring during maternal feedings we tried to discern whether active maternal discrimination between son and daughter was a plausible mechanism involved in mother-offspring interactions. Specifically, we looked for (a) aggressions, (b) refusals to feed a soliciting chick, (c) differential maternal feeding rates when both siblings solicited food under identical circumstances, i.e. when they (c1) started a begging approach to the mother from identical distances to her, or (c2) approached her simultaneously (see specific parameters in Tables 1 and 2). In addition, to evaluate whether the consequences of these mother-chick interactions could be relevant for population sex ratio as predicted

by sex allocation theory, we examined whether mortality differed between siblings in mixed-sex broods. According to the differential mortality hypothesis, we should expect a higher mortality of male siblings, which are much larger and thus more vulnerable to starvation than their sisters (Clutton-Brock et al., 1985; Stamps, 1990; Clutton-Brock, 1991; Kalmbach & Benito, 2007).

In principle, the great bustard should be a good candidate to expect differences in good condition mothers' expenditure in sons and daughters. First, this lekking species shows the highest sexual size dimorphism among birds (Alonso et al., 2009). Strong sexual dimorphism develops very early during juvenile development, suggesting that rapid growth of young males is evolutionarily selected (Alonso et al., 2009). Second, young birds are precocial and feed themselves shortly after hatching, but have prolonged maternal dependence periods (6-18 months), during which they receive additional feedings from the mother (Alonso & Alonso, 1992; Alonso et al., 1998). As in some polygynous ungulates, in great bustards we found evidence of maternal care having a critical influence on the breeding success of sons but not of daughters. Young males that fed at higher rates or received more feedings from their mothers became independent at a younger age, integrating earlier into adult male flocks, and settling earlier at their definitive leks, which suggests clear fitness advantages from an early maternal care (Alonso et al., 1998). These relationships were not found in young females. However, these benefits of rapid growth are counterbalanced by a higher male mortality from starvation when food is scarce (Martín et al., 2007), which determines a female-biased sex ratio that appears at an age of 2-3 months and continues into adulthood in all populations (Alonso et al., 2003, 2005a,b). Finally, the great bustard is also highly polygynous, with probably the strongest documented skew in male mating success among birds, and weight being one of the main factors favouring a high rank of males within the lek and facilitating their access to females (Alonso et al., 2010).

METHODS

Study Area and Species

The study was conducted in the Wildlife Reserve Lagunas de Villafáfila (33000 ha), northwest Spain. The climate is characterized by hot, dry summers, rainy autumns and springs and cold winters. The landscape is treeless and flat to gently undulating, and consists of extensive, two-year-rotation dry cereal farmland (ca. 80% of the surface),

with alfalfa fields (8%), pasture land (7%) used for sheep grazing, and scattered vineyards and other minor crops (5%) (details in Alonso & Alonso, 1990).

Male and female great bustards live in separate flocks all year round, and meet in early spring at traditional lek arenas, where males display to attract females. After mating in April, most males abandon the lek site, while females take on all breeding duties. The chicks depend on their mother for 6-18 months (Alonso et al., 1998). They follow her at close distance and remain isolated from other non-breeding or unsuccessfully breeding females until late September, when they start flocking with other females (Martín, 1997). The first months of life are crucial for the development and survival of male chicks, and also for their future success as adults (Alonso et al., 1998, 2010). Young males grow much faster than young females soon after hatching, being significantly heavier at an age of only ten days (Litzbarski et al., 1983). The early appearance of sexual size dimorphism allows experienced observers to distinguish the sex of chicks at an age of just a few weeks, and unmistakably during August-September, when chicks are 2-4 months old (Martín, 1997; Alonso et al., 2005, 2009).

Mother-chick Feeding Interactions and their Effect on the Mother's Intake Rate

Between mid August and early October 1993-1994 we searched for families with two chicks. These are uncommon, since (a) on average, only one out of 8-10 females is successful in rearing chicks up to that age, and (b) only ca. 15% of all successful females have two chicks in September, with older, more experienced females showing a clear tendency to have higher breeding success (Morales et al., 2002; Magaña, 2007). We located 48 families (27 mixed-sex broods, 8 with two male chicks, and 13 with two female chicks), and accumulated a total of 40 hours and 39 minutes of simultaneous observation of all members of these families. Two-chick broods represent the two scenarios in which the Trivers-Willard hypothesis should apply, namely that of parents in good condition, and that of years with more resources. We could indeed reasonably guess that (a) our sample included high quality mothers, since all had two offspring, and (b) if annual juvenile productivity is taken as a reliable indicator of food abundance, we can guess that resources were abundant during both study years (0.14 chicks/female in 1993, and 0.27 in 1994; mean \pm SD productivity for 1987-1995: 0.14 \pm 0.09 chicks/female; Morales et al., 2002), and particularly in 1994, the year when we did the detailed study of mother-offspring interactions in 11 families with mixed-sex offspring (see below, penultimate paragraph of this section).

In order to avoid the influence of changes in patterns with chick's age we reduced the study period to just one and a half months. Because our main interest was to measure feeding rate differences between siblings, we restricted data collection to the period of maximum foraging activity in the early morning and evening hours (Martín, 1997). When a two-chick family was located, we recorded the behavior of mother and offspring continuously during 30-min, a period long enough to detect differences in relevant parameters (Table 1). We observed the birds using telescopes 20-60x or 60-90x, from a distance of 500m to >1000m to avoid disturbing them. The scarce vegetation provided excellent observation conditions which allowed keeping focal birds within field of vision over the observation period. Of each mixed-sex brood we recorded one to seven 30-min observation periods distributed over the 1.5-months study period, with a mean of 64.5 minutes total observation time per family. The values obtained in all 30-min periods of a given family were later averaged to obtain mean values for that family. Since in same-sex broods the identification of both chicks was not guaranteed on successive visits, in these families we decided to record only a single 30-min observation period. A size difference was very apparent only in four same-sex families, and less evident but still perceptible in another three. In these cases, we named the largest as sibling 1. In the remaining fourteen families, we defined as sibling 1 the closest to the mother when we started the observations.

During each observation period, we recorded the following variables (see Table 1): *Maternal feeding rate*: number of times per minute the mother took food and offered it to her offspring while holding it in her beak; *Maternal food signaling rate*: number of times per minute the mother pointed with her beak to a food item found on the ground to induce offspring to eat it; *Consecutive maternal feedings*: average number of maternal feedings received by the same chick in succession, i.e. without interruptions to feed the other chick, during the 30-min observation period; *Chick intake rate*: number of times per minute the chick took food from the ground by itself, without participation of the mother; *Distance mother-chick*: mean distance in meters -estimated based on body lengths-between chick and mother at the start of every minute throughout the 30-min observation period; *Period closer to mother than sibling*: continuous time a chick remained closer to the mother than its sibling (both chicks alternated in staying closer to the mother for periods varying between one and thirty minutes); *Time closer to mother than sibling*: percentage of the total observation period when the chick was closer to the mother than its sibling (after discounting the time when both siblings were at the same

distance from their mother); *Maternal feeding rate when closer to mother*: calculated dividing the number of consecutive maternal feedings by the period closer to mother than sibling.

To quantify the effect maternal expenditure in her son and daughter might have on her own feeding rate, we measured the *Absolute intake rate of the mother* (= total ingestions of the mother / total observation time), and the *Net intake rate of the mother* (= total ingestions of the mother / total time mother spent feeding).

In order to study the details of mother interactions with her male and female offspring, in 1994 we randomly chose a subsample of 11 families with mixed-sex broods for which observation conditions were particularly favorable, and recorded the following data of a total of 370 maternal feedings (Table 2): *Begging success (%)*: percentage of begging approaches from chick to mother that resulted in a feeding; *Begging success when closer to mother than sibling (%)*: percentage of begging approaches from chick to mother that resulted in a feeding, when that chick started the approach from a closer distance to the mother than its sibling; *Begging success in simultaneous approaches when both start from the same distance (%)*: percentage of begging approaches that resulted in a feeding, when both chicks started from the same distance and approached the mother simultaneously.

In addition to the main study of two-chick broods, and as a further control of the differences in maternal feeding rates to sons and daughters in these families, we used the results on *Maternal feeding rate* and *Chick intake rate* of a sample of 26 single-chick broods (15 with a female chick, 11 with a male chick) included in our unpublished radio-tracking study of the mother-chick relationships carried out in 1991-1994 at Villafáfila Reserve (Martín, 1997). Although the observation method in that study (3-minutes recording of intake rate and maternal feeding rate every 30 minutes during all-day observation periods, one observation day per family every week throughout the first twelve months of life of the chicks) differed from that used for two-chick broods, we filtered data to cover the same periods of the day (early morning and evening hours) and months (mid August to early October) as in the study of two-chick families (see above).

Offspring Mortality

In July 1987-1993 we marked 45 chicks in 27 two-chick families in Villafáfila Reserve (26 chicks in 16 mixed-sex broods, 7 in 5 same-sex male broods, and 12 in 6

same-sex female broods). Our aim was to examine sex differences in age of death in mixed-sex broods, and body condition-related differences in age of death in same-sex broods. As a body condition index we used body mass divided by tarsus length (Labocha & Hayes, 2012). We excluded cases when mortality was due to causes clearly not related to maternal care, such as collision with power lines. To achieve a larger sample we also used mortality data of 71 chicks marked between 1995 and 2003 in two-chick broods in Madrid province (IBA Talamanca-Camarma, 52981 ha), ca. 250 km southeast of Villafáfila (data from Martín et al., 2007), plus 56 chicks marked in two-chick broods in that area in 2004-2013 (JC Alonso et al., unpubl. data). For mortality analyses we discarded families with inaccurate mortality dates for one of the chicks, or those in which we could not calculate the body condition of one of them (see below). Therefore, our total sample for mortality analyses was 38 mixed-sex broods (10 in Villafáfila, 28 in Madrid), 5 same-sex broods of two male chicks (1 in Villafáfila, 4 in Madrid), and 17 same-sex broods of two female chicks (2 in Villafáfila, 15 in Madrid). To allow birds to adapt to wearing wing-tags and transmitters we only included in our analyses those birds that survived the week immediately after marking (Villafáfila: 93% of marked males, 95% females; Madrid: 93% males, 89% females). We found no significant differences in the survival of radio-tagged and untagged young between early and late summer (tagged: 58%; untagged: 62%; $\chi^2 = 1.85$, $df = 1$, $P = 0.174$; see details in Martín et al., 2007).

We captured the birds in July by chasing them down using a vehicle to make them fly once or twice, and later by running to them when they laid down and tried to go unnoticed by remaining motionless on the ground. No adverse effects of that capture method were observed, and all chicks joined their mother once released after a marking process lasting 10-15 minutes (see Martín et al., 2007). We marked the birds with wing-tags and radio-transmitters (small females with Biotrack TW3 2x2/3AA 30 g neck-lace units, larger females and all males with TW3 2xAA 60 g backpack-mounted units, other details in Martín et al., 2007). We used elastic harness material to allow the harness to expand as the young grew. The total weight of transmitter plus harness did not exceed the recommended limit of 3-5% of the bird's weight (Kenward, 2001). All marked birds were located 2-3 times per month during the first two months and at least once monthly throughout their lives, using Telonics TR2-TS1 telemetry receivers and aircraft for aerial location after juvenile dispersal. The date of death was estimated through the degree of decomposition of the carcass. When we only found remains such as a few

feathers or bones, or just the transmitter, we assumed the date of death as the midpoint between the last time the bird had been controlled alive and the date when the remains were found. The interval between these two dates did not usually exceed 30 days (details in Martín et al., 2007).

Statistical Analyses

We used Wilcoxon's matched pairs tests to assess differences between siblings in all variables (maternal feeding and food signaling rate, number of consecutive maternal feedings, chick intake rate, distance mother-chick, and time closer to mother than sibling), in the three types of families studied: mixed-sex broods (27 families), same-sex broods with two male offspring (8 families) and same-sex broods with two female offspring (13 families). To check for differences in chicks of the same sex between different family types, we used Mann-Whitney U tests. We used Spearman's rank correlations to assess relationships between variables using the mean values for each family as data points. Finally, we used Chi-squared tests to examine differences in the probabilities of an earlier death between male and female siblings, or between the siblings showing a better and a worse body condition.

We also used Wilcoxon's matched pairs tests to examine the differences between male and female siblings in the mean values per family ($N = 11$ families, year 1994) of variables describing the outcomes of the 370 maternal feedings. Based on that analysis, we defined the following two indices to account for factors that appeared to be more relevant in the begging approach and begging success of the chicks: (i) *Relative proximity of male chick to mother*, defined as the distance between male chick and mother divided by the distance between female chick and mother; and (ii) *Relative begging approach intensity of male chick to mother*, defined as the determination (= number of steps/distance chick-mother in meters) at which the male chick approached the mother when she held a prey in the beak, divided by the intensity at which the female chick approached the mother. This 'begging approach intensity' index was relevant in cases when both chicks were at similar distances from the mother, or when the closest chick showed less conviction or was more hesitant in the approach, most probably because it had been fed several times and was presumably satiated, and therefore did a much lower number of steps than its farther but hungrier sibling. To avoid zero values in the numerator of this index (i.e., include a few cases when the chick was immediately besides the mother and did not have to walk to her), we added

0.01 to the number of steps. Values equal to 1 in these two indices indicated identity between male and female chicks, values higher than 1 indicated respectively, closer distance of female chick to mother (index i), and higher approach intensity of male chick (index ii). We could measure the numbers of steps of both chicks using two manual counter clickers. We tested for the effect of these two indices and their interaction on the outcome of each feeding event by means of a Generalized Linear Model (GLM) with binomial distribution (1 = male chick was fed, 0 = female chick was fed), using all 370 maternal feedings as data points and including family as a random factor. We included the interaction to account for the few cases when both chicks started their approach from an equal distance to the mother and performed simultaneous approaches, under the assumption that in such cases the determination to approach the mother could be the relevant factor leading to a successful begging. All analyses were performed using Statistica v. 7.

RESULTS

Differences between Siblings in Feeding Rates and Distance to Mother

In mixed-sex broods, male chicks received twice the number of maternal feedings per unit time than their female siblings (Table 1). The frequency of food signaling events from the mother towards male chicks also doubled that directed towards female chicks (Table 1). The mean number of consecutive maternal feedings received by male chicks was higher than that received by female chicks (Table 1). Male chicks stayed on average two meters (28%) closer to their mother than female chicks (Table 1). Both chicks alternated in staying closer to the mother during periods varying between one and thirty minutes, but these periods were on average longer in male chicks, which resulted in a longer total time spent closer to the mother (67.4% of total time, compared to 32.6% in female chicks; Table 1). The differences between male and female chicks in maternal feeding rate disappeared when considering only periods when the chick was closer to the mother than its sibling (respectively, 0.71 and 0.69 feedings/min; Table 1). Finally, male chicks also fed by themselves at a 17% faster rate than their female siblings, although this difference was not statistically significant after Bonferroni correction (Table 1).

In same-sex broods, siblings did not differ either in the feeding rates received from the mother, or in their own intake rates (Table 1). The only apparent differences were found in the time each chick spent closer to the mother, but these differences were

not statistically significant after Bonferroni correction for multiple comparisons (Table 1). Neither in mixed-sex, nor in same-sex families did we observe any maternal aggression or refusal to feed a soliciting chick.

Table 1

Differences between siblings in their own food intake rate, various parameters reflecting the number and intensity of feedings received from their mother, and mean distance and percent time spent close to her

Variable	Mean \pm SD		Test of difference ¹		
<i>Families with two offspring of different sex (mixed-sex broods, N = 27):</i>					
	Male offspring	Female offspring	Z	P	significance ²
Maternal feedings/min	0.16 \pm 0.20	0.08 \pm 0.12	2.94	0.003	*
Food signalling events/min	0.13 \pm 0.11	0.07 \pm 0.06	3.16	0.002	*
No. consecutive maternal feedings	3.77 \pm 2.56	2.08 \pm 1.10	3.74	0.002	*
Average distance mother-chick (m)	4.90 \pm 1.90	6.80 \pm 2.70	3.74	< 0.001	*
Average period closer to mother than sibling (min) ⁴	7.09 \pm 5.68	3.77 \pm 2.62	2.62	0.006	*
Time closer to mother than sibling (%)	67.4 \pm 21.5	32.6 \pm 21.5	3.20	0.001	*
Maternal feeding rate when closer to mother (feedings/min) ⁵	0.71 \pm 0.43	0.69 \pm 0.46	1.12	0.26	NS
Chick intake rate (ingestions/min)	16.9 \pm 7.68	14.5 \pm 6.49	1.90	0.05	NS
<i>Families with two male offspring (N = 8):</i>					
	Sibling 1 ³	Sibling 2 ³	Z	P	
Maternal feedings/min	0.13 \pm 0.20	0.07 \pm 0.05	1.10	0.27	NS
Food signalling events/min	0.11 \pm 0.09	0.09 \pm 0.06	1.05	0.29	NS
No. consecutive maternal feedings	2.64 \pm 2.85	2.43 \pm 1.27	0.59	0.55	NS
Average distance mother-chick (m)	5.65 \pm 1.91	6.40 \pm 1.90	1.86	0.06	NS
Average period closer to mother than sibling (min) ⁴	5.08 \pm 2.03	5.11 \pm 4.91	1.18	0.23	NS
Time closer to mother than sibling (%)	63.1 \pm 12.7	36.9 \pm 12.7	1.99	0.05	NS
Maternal feeding rate when closer to mother (feedings/min) ⁵	0.50 \pm 0.45	0.75 \pm 0.58	0.51	0.61	NS
Chick intake rate (ingestions/min)	31.3 \pm 14.55	26.1 \pm 15.01	0.28	0.78	NS
<i>Families with two female offspring (N = 13):</i>					
	Sibling 1 ³	Sibling 2 ³	Z	P	
Maternal feedings/min	0.04 \pm 0.05	0.04 \pm 0.05	0.68	0.50	NS
Food signalling events/min	0.05 \pm 0.05	0.06 \pm 0.06	0.83	0.41	NS
No. consecutive maternal feedings	1.69 \pm 0.97	1.93 \pm 1.06	1.05	0.29	NS
Average distance mother-chick (m)	5.50 \pm 2.28	5.93 \pm 2.09	1.37	0.17	NS
Average period closer to mother than sibling (min) ⁴	6.23 \pm 4.83	3.42 \pm 1.03	1.96	0.05	NS
Time closer to mother than sibling (%)	59.5 \pm 9.9	40.5 \pm 9.9	2.55	0.01	NS
Maternal feeding rate when closer to mother (feedings/min) ⁵	0.40 \pm 0.27	0.56 \pm 0.32	1.60	0.11	NS
Chick intake rate (ingestions/min)	15.9 \pm 9.03	14.6 \pm 10.90	1.37	0.16	NS

¹ Wilcoxon's matched pairs test; ² significance after Bonferroni correction marked with an asterisk, NS = not significant after Bonferroni correction ³ In the seven families where a clear

size difference was appreciated between both chicks, the largest was defined as sibling 1; in the remaining 14 families, sibling 1 was the closest to the mother at the start of the observations; ⁴Both chicks alternated in staying closer to the mother during 1-30 min periods; this is the mean duration of these time periods for each; ⁵ Calculated dividing the number of consecutive feedings by the period closer to mother than sibling

Correlations between Parameters

The study of correlations using mean values per family provided some noteworthy results. First, in mixed-sex broods, only in the male chick, but not in the female chick did the mean number of consecutive maternal feedings show correlation with the mean time spent closer to the mother than its sibling (male chick: $r_s = 0.50$, $P < 0.02$; female chick: $r_s = 0.12$, ns). Second, in mixed-sex broods, the number of maternal feedings plus food signaling actions to the daughter was negatively correlated with the time the brother remained closer to the mother ($r_s = -0.40$, $P < 0.05$); but the equivalent correlation between maternal feedings to the son and time its sister remained closer was not significant ($r_s = -0.22$). None of these relationships were significant for any of the chicks in same-sex broods (respectively, $r_s = 0.09$, $r_s = 0.13$; $r_s = -0.14$; $r_s = -0.12$). These results suggest that the feeding rate of a female chick decreases when her brother is closer to the mother, something that does not happen with any of both siblings when they are of the same sex.

Finally, in two-chick broods with at least one male chick, i.e. those with male and female siblings plus those with two male siblings, there was a negative correlation between maternal feeding rate to both chicks and the mother's own net feeding rate ($r_s = -0.32$, $P = 0.06$ with maternal feeding rate to sibling 1; $r_s = -0.57$, $P < 0.001$ with maternal feeding rate to sibling 2). The equivalent correlations were far from being significant, or even positive in some cases, in families with no male chick ($r_s = -0.01$, $P = 0.96$, and $r_s = 0.17$, $P = 0.58$, between the mother's own net feeding rate and, respectively, female chick 1 and female chick 2; $r_s = -0.18$, $P = 0.55$, and $r_s = 0.02$, $P = 0.94$, between the mother's own absolute feeding rate and, respectively, female chick 1 and female chick 2). These results suggest that rearing male chicks is more costly to the mother than rearing female chicks.

Differences between Two-chick Family Types in Mother-chick Parameters

When we compared the parameters describing mother-chick relationships among families of different types we found a few remarkable differences. First, in mixed-sex broods the male chick received more consecutive maternal feedings than male sibling 1 in broods of two males (3.77 vs 2.64, $Z = 1.92$, $P = 0.05$; Mann-Whitney U-test; $N_1 = 27$, $N_2 = 8$; Table 1). Second, in mixed-sex broods the female chick spent less time closer to the mother than female sibling 2 in broods of two females (32.6 vs 40.5% time, $Z = 2.01$, $P = 0.04$; Mann-Whitney U-test; $N_1 = 27$, $N_2 = 13$; Table 1). This did not result in a lower maternal feeding rate to the female chick in mixed-sex broods compared to female sibling 2 in all-female broods (0.08 vs 0.04, $Z = 1.37$, $P = 0.18$; Table 1), but suggested that the time female chicks of mixed-sex broods spent close to the mother could be limited by the time their brothers stayed by the mother. Interestingly, maternal feeding rate and food signalling events did not differ between sibling 1 of two-male broods and sibling 1 of two-female broods (respectively, $Z = 1.15$, $p = 0.27$, and $Z = 1.67$, $P = 0.10$; Mann-Whitney U-test; $N_1 = 27$, $N_2 = 13$; Table 1), sons from mixed-sex broods and sibling 1 of two-male broods (respectively, $Z = 0.96$, $P = 0.33$; $Z = 0.31$, $P = 0.75$), and daughters from mixed-sex broods and sibling 1 of two-female broods (respectively, $Z = 1.40$, $P = 0.16$; $Z = 0.20$, $P = 0.84$). Overall, differences between male and female chicks in mixed-sex broods were stronger than those between siblings in same-sex broods.

Differences between Male and Female Siblings in Begging Success

As a rule (356 of the 370 feedings recorded in the 11 mixed-sex families of Table 2), the chick standing closer to the mother when she offered a prey was the one that obtained the feeding. In the remaining 14 cases, i.e. when the successful chick started its begging approach from a farther distance to the mother than its sibling, that chick invariably approached the mother with higher *intensity* (more steps/distance chick-mother) than its sibling. The success of the farthest chick in simultaneous approaches of both siblings was also extremely rare (found only in two families, one favouring each sex). Since brothers stay longer by the mother than sisters (Table 1), it is logical that there were 43.5% only-male begging approaches, compared to 29.1% only-female begging approaches (in 20.4% of the cases both chicks approached, and in 7% of the cases both chicks were so close to her mother that no approach was needed when she offered a prey). We found more families in which the male chick was more successful than its sister (8 vs 1), and mean begging success values of brothers were

higher than those of sisters (92.1% vs 71.4%; Table 2). However, the significance of these differences in favour of males disappeared when we examined those cases where the successful chick started the approach from a closer distance to the mother than its sibling (98.3 vs 89.5 success respectively in male and female chicks; 5 vs 2 families; Table 2). In the five families in which we observed cases of both siblings approaching the mother simultaneously, starting from the same distance, it was typically the male chick who obtained the feeding (93.3% vs 6.7%; Table 2). This was because in most of these cases the male chick was faster in the approach than its sister (reached the mother earlier in 80% of the cases vs 10% cases when the sister arrived earlier).

The GLM analyzing these 370 maternal feedings confirmed that the closer proximity of male chicks to the mother was the significant factor explaining their higher begging success compared to their female siblings (Table 3). The significant interaction between proximity and approach intensity suggests that the higher determination when approaching the mother was also relevant in cases of equal, or sometimes even farther distance to the mother (Table 3).

Table 2

Differences between male and female siblings in various measures of offspring begging success in a sample of 370 maternal feedings recorded in 11 families with one chick of either sex

	Mean \pm SD		No. of families with higher value in male/female chick ¹		Test of difference ²	
	Male chick	Female chick	Male chick	Female chick	Z	P
Begging success (%) ³	92.1 \pm 10.2	71.4 \pm 22.6	8	1	2.09	0.037
Begging success when closer to mother than sibling (%) ⁴	98.3 \pm 3.7	89.5 \pm 14.7	5	2	1.52	0.128
Begging success in simultaneous approaches when both start from the same distance (%) ⁵	93.3 \pm 14.9	6.7 \pm 14.9	5	0	2.02	0.043

¹ These are the numbers of families in which either the male or the female chick had higher mean values of each parameter; the remaining families that would complete the sample of 11 had either equal mean values for male and female chicks, or no cases for that parameter; ² Wilcoxon's matched pairs test comparing absolute numbers of beggings for each sex within

each family; ³ Percentage of begging approaches from chick to mother that resulted in a feeding; ⁴ Percentage of begging approaches from chick to mother that resulted in a feeding, when that chick started the approach from a closer distance to the mother than its sibling; ⁵ Percentage of begging approaches that resulted in a feeding, when both chicks approached the mother simultaneously, starting from the same distance

Table 3

Results of the generalized linear model (GLM) analyzing the 370 maternal feedings recorded in the 11 families observed in detail (see Table 2). Dependent variable: 1 = mother feeds male chick; 0 = mother feeds female chick; the model was highly significant ($F_{3,366} = 82.24$, $P < 0.001$)

	SS	df	MS	F	P
Intercept	99.39	1	99.39	787.86	0
Relative proximity of male chick to mother ¹	16.64	1	16.64	131.92	< 0.001
Relative approach intensity of male chick to mother ²	0.07	1	0.07	0.57	0.450
Interaction relative proximity x relative approach intensity	3.90	1	3.90	30.93	< 0.001
Error	46.17	366	0.13		

¹ distance between male chick and mother divided by the distance between female chick and mother; ² intensity (= number of steps/distance chick-mother in meters) with which the male chick approached the mother, divided by the intensity with which the female chick approached the mother when she held a prey in the beak

Mortality Differences between Siblings

In mixed-sex broods, an earlier death of the female chick was more probable than an earlier death of the male chick (respectively, 9 families vs 1 family in Villafáfila, $\chi^2 = 3.81$, $P = 0.05$; 30 families vs 6 families in the whole sample of Villafáfila + Madrid, $\chi^2 = 9.00$, $P = 0.003$). In families of two chicks of the same sex, the chick showing a worse body condition at the time of marking tended to die earlier than its sibling with better body condition (respectively, 18 vs 5 cases, $\chi^2 = 3.92$, $P = 0.048$ in Villafáfila + Madrid; the sample for only Villafáfila was too small to be analyzed).

Differences in Feeding Rate between Two-chick and Single-chick Broods

Female chicks in mixed-sex broods received maternal feedings at a significantly lower rate (0.08 ± 0.12 feedings/min, $N = 27$, see Table 1) than female chicks in single-

chick broods (mean \pm SD: 0.13 ± 0.09 feedings/min, $N = 15$; Mann-Whitney U-test, $Z = 2.61$, $P = 0.009$). In single-chick broods, maternal feeding rate to female chicks did not differ significantly from that to male chicks (mean \pm SD: respectively, 0.13 ± 0.09 feedings/min, $N = 15$; 0.15 ± 0.14 feedings/min, $N = 15$; Mann-Whitney U-test, $Z = 0.21$, $P = 0.83$). However, in spite of this small difference in the feeding rate per minute, single-male chick families spent more time foraging than single-female chick families, resulting in a total number of maternal feedings per day being a 28% higher in single-male than in single-female broods (mean \pm SD: respectively, 31 ± 39 feedings, $N = 15$; 24 ± 20 feedings, $N = 11$), and a total daily food intake being significantly higher in single-male than single-female chicks (mean \pm SD: respectively, 4686 ± 1611 ingestions per day, $N = 15$; 2733 ± 1669 ingestions per day, $N = 11$; Mann-Whitney U-test, $Z = 2.78$, $P = 0.005$).

DISCUSSION

In mixed-sex broods, male chicks received twice the number of feedings and food signaling actions from their mother per unit time than female chicks. Our results suggest that this male-biased feeding rate was a direct consequence of the longer periods male chicks stayed closer to the mother. These were on average almost twice as long as those of their sisters and resulted in male chicks spending twice as much time per day closer to the mother. By remaining closer, male chicks seemed to have priority over their sisters in accessing the mother when she offered a feeding. These conclusions were supported by the lack of similar patterns in same-sex broods, where there were no significant differences between siblings in time spent closer or mean distances to the mother, nor in any of the feeding parameters. The fact that female chicks of single-chick broods received significantly more maternal feedings per minute than female chicks of mixed-sex broods suggests that the presence of a brother could be the crucial factor determining the reduced maternal feeding rate to female chicks in mixed-sex broods.

We observed no signs suggesting that mothers of mixed-sex broods preferred to feed male chicks over female chicks. First, feedings always occurred after an active begging approach from a chick when the mother held a prey in her beak, but she consistently remained still and waited for one or both chicks to approach, never refusing to feed the chick approaching first. Second, maternal feeding rate to both chicks was proportional to the time each chick spent closer to her than its sibling, and the rates at which a mother fed son and daughter when each stayed closer to her than the twin were

506 remarkably similar. Third, although the overall *Begging success* was higher in male
507 chicks, *Begging success when closer to mother than sibling* was practically identical in
508 brothers and sisters. Fourth, brothers had a higher begging success in simultaneous
509 approaches from the same distance because they approached the mother at a faster
510 speed than their sisters, and not due to any maternal preference. Finally, in the few cases
511 when the successful chick was the one starting the approach from a farther distance to
512 the mother (14 out of 370 cases), its determination when running towards the mother
513 was higher than that of its twin. The GLM results confirmed that the interaction
514 between approach intensity and proximity to the mother was significant, and that both,
515 proximity and its interaction with approach intensity were decisive in determining a
516 higher begging success in male chicks.

517 Maternal manipulation is neither supported by mortality or sex-ratio patterns in
518 great bustards. Clutton-Brock (1991) suggested that when parental manipulation is
519 involved, mortality should be expected to happen early in the parental care period, to
520 minimize wastage of resources. Possible mechanisms may be egg size or egg sex-ratio
521 manipulation (Nager et al., 1999), sex-specific hatching order control (Bortolotti, 1986;
522 Dzus et al., 1996), or hormone leakage from mother to fetuses (reviewed in Uller,
523 2006). In one of the best documented examples of sex-biased mortality related to
524 maternal costs in ungulates, 85% of calves died within two weeks of birth, implying
525 minimal lactation costs to mothers (Froy et al., 2016). In great bustards, data from a
526 different population to that studied here on sex differences in weight and sex bias at
527 hatching do not support the early mortality predicted when maternal manipulation is
528 involved. Male and female hatchlings did not differ in weight (males = 91.6 g, $N = 185$;
529 females = 91.9 g, $N = 192$; H Litzbarski, pers. comm.), and sex ratio at hatching was not
530 biased (1 male: 1.04 females, $\chi^2 = 0.188$, $df = 1$, $P = 0.67$, $N = 531$ eggs collected for
531 artificial breeding at Buckow Station, Germany, 1979-1998; H Litzbarski, pers. comm.).
532 Moreover, male-biased offspring mortality increased during the second half of the early
533 development period of the chicks compared to the first half (1 male : 1 female at
534 hatching in early June; 1 male : 1.24 females by mid July; and 1 male : 1.80 females by
535 mid September, 1995-2003; Martín et al., 2007).

536 We conclude that in great bustards there is no need to invoke maternal
537 preference for either of the chicks. Our study supports the more parsimonious
538 hypothesis that male-biased maternal feeding rate is determined by the higher food
539 requirements of male chicks due to their faster growth rates (Alonso et al., 2009), which

implies that the bias would be ultimately determined by sexual selection, without any manipulation by the mother. Studies on some highly dimorphic mammals also concluded that differential investment in male and female offspring may result from evolution acting on the competitive ability of the offspring to manipulate the amount of food or care transferred from the mother, rather than on mother's preferences (Kovacs & Lavigne, 1986; Lee & Moss, 1986; Kretzmann et al., 1993). As for the mechanism operating, we only observed one aggression between siblings, from a male chick to its sister, so we don't know whether the dominance of male chicks remains unchallenged by their sisters simply by their noticeable differences in size. Our results suggest that the smaller female chicks become outcompeted by their brothers, who probably just by remaining longer close to the mother, prevent sister siblings from taking a higher share of maternal feedings. Such competitive exclusion was not detected in broods of the same sex, where size differences between siblings are much smaller or non-existent. The negative effect of having a brother was also supported by the significantly higher maternal feeding rate of female chicks in single-chick broods, where sex differences between siblings were absent. The 24% shorter time spent closer to the mother by female chicks with a brother compared to female chicks with a sister supports our conclusion that occupation of the space around the mother by male chicks is the most important mechanism preventing female chicks of mixed-sex broods from accessing the mother.

In many birds, size is an important determinant of offspring sex asymmetries in competitive ability (reviews in Mock, 1984, 1985; Stamps et al., 1985, 1989; Mock & Parker, 1997; Drummond, 2001), and larger siblings sometimes attack or even kill smaller siblings (Drummond et al., 1986; Mock et al., 1987). But the best examples of direct competition between male and female twins are from mammals (Burfening, 1972; Clutton-Brock & Albon, 1982; Korsten et al., 2009), including humans (Lumma et al., 2007; but see Medland et al., 2008). Most authors discarded parental manipulation as an explanation, and reviews suggest that most cases of sex-biased parental investment may be a by-product of sexual selection acting on offspring (Clutton-Brock, 1991; Redondo et al., 1992; Cockburn et al., 2002; Krackow, 2002; Uller, 2006).

The female-biased mortality found in mixed-sex broods was an unexpected result, since juvenile mortality is normally male biased in this species (Martín et al., 2007). However, this result indeed supports our conclusion that the female chick disadvantage when sharing maternal food provisioning with her brother may be the

relevant mechanism involved, the ultimate consequence being the death of the female offspring from starvation if food is scarce. In many other birds and mammals showing a marked male-biased sexual size dimorphism, the largest sex typically suffers higher mortality (Clutton-Brock et al., 1985; Stamps, 1990; Clutton-Brock, 1991; Kalmbach & Benito, 2007), but at least in some altricial birds the smaller sex has also been found to suffer higher mortality or stunted growth (Anderson et al., 1993; Oddie, 2000; Raberg et al., 2005; Kalmbach & Benito, 2007). Recent studies with mammals have shown that having a male twin reduces birth weight and first-year survival in their sisters, due to direct competition between fetuses (Wilson et al., 2005; Korsten et al., 2009). In great bustards, the role mothers could play in male-biased survival in mixed-sex broods remains unclear and deserves further study, but our observations do not suggest that mothers would reject their daughters' begging attempts up to starvation. Thus, the priority of male siblings in accessing maternal feedings remains the most likely explanation.

The higher mortality of sisters in mixed-sex broods raises the question whether these broods could be selected against because they lead to brood reduction (reviewed in Cockburn et al., 2002; Uller, 2006; see also Korsten et al., 2009). In great bustards, however, there is no evidence of a bias against mixed-sex broods in a 26-year sample (Male-Male : Male-Female : Female-Female broods = 48 : 119 : 54; $\chi^2 = 1.63$, $df = 2$, $P = 0.44$, compared to the expected ratio 50 : 100 : 50; $N = 221$ families, identified in 23 surveys carried out in our study areas in early July 1987-2013; although this bias should ideally be checked at hatching, before any mortality occurs, sexes cannot be reliably distinguished, and most families are hidden in the unharvested cereal before early July).

The slight differences in time spent closer to the mother between two brothers or two sisters of same-sex broods did not result in significant differences in maternal feeding rates, but were indeed enough to detect a higher mortality of siblings in worse condition. Overall, these results suggest that direct sibling competition for food may also be the relevant mechanism in these broods, probably without any active brood reduction promoted by the mother.

Two results from the correlation analysis of mean family values suggest that the advantages gained by male chicks through prolonging the periods closer to the mother may represent an exclusive mechanism of male chicks when they have sisters, and not when they have brothers, nor of female chicks in either mixed- or same-sex broods. First, overall maternal feeding rate and mean number of consecutive maternal feedings

were correlated in both, mixed-sex and same-sex broods. As we discussed above, prolonging each period closer to the mother is an efficient mechanism to get more feedings. However, only in male chicks with sisters was the mean number of consecutive maternal feedings correlated with the mean time they spent closer to the mother, whereas that correlation was neither found in their sisters, nor in either of the siblings in same-sex broods. Second, only in mixed-sex broods was there a negative correlation between time spent by the female chick close to the mother and average distance brother-mother. That correlation was not found in same-sex broods. These results support our conclusion that in mixed-sex broods the male chick obtained more maternal feedings by monopolizing the mother's attention, i.e. by remaining longer time closer to her. A similar asymmetric competition system between sexes has been described for Soay sheep twins, where female but not male fetuses are affected by male co-twins (Korsten et al., 2009).

Finally, the correlation analysis provided evidence of a higher cost incurred by a mother when rearing male chicks. In broods with at least one male chick, the mother's own net feeding rate decreased as the maternal feeding rate to both chicks increased, whereas these correlations were completely absent in broods with no male chick, suggesting a much smaller maternal cost in the latter. We do not find a completely convincing explanation for the lower significance of the negative correlations between the mother's feeding rates and her maternal feeding rate to male sibling 1 vs that to male sibling 2, but a reasonable suggestion would be that rearing just one male chick does not represent a very high cost to mothers, whereas adding a second male chick means a significant additional cost, and eventually determines the higher mortality found in two-male broods commented above. It is tempting to speculate that this result might represent a direct empirical support to the hypothesis that maternal feeding capacity is limited to a maximum of two male chicks. Martín (1997) found that mothers could devote significantly less time to feeding than non-breeding females, resulting in a lower daily food intake in mothers. Significant differences with non-breeding females disappeared only when chicks were 8-9 months old. This clearly shows that rearing chicks represents a significant cost to mothers.

In single-chick families, maternal feeding rate to sons remained slightly higher than that to daughters up to September, when chicks are three to four months old, but turned to be slightly higher to female chicks between October and February, when the last maternal feedings occur (Martín, 1997). However, neither each monthly rate

considered separately, nor the overall maternal feeding rate considering the whole dependence period, were significantly different between male and female chicks in these families (Martín, 1997). Martín's (1997) results and those of the present study suggest two conclusions. First, both studies provide evidence that the cost to mothers of rearing male chicks is higher than that of rearing female chicks, but only during the first months of life of the chicks, when the growth rate of male offspring is really fast and critical for their future success as adults (Alonso et al., 1998, 2009). The higher maternal expenditure on male chicks during this phase is compensated by a higher expenditure on female chicks during the rest of the dependence period, once that critical early development phase of male offspring is over, and many young males are getting already independent while most female chicks still remain with their mothers (Alonso et al., 1998). A more prolonged maternal investment period in daughters has also been described for several mammals, where the higher investment in sons before weaning may also be balanced by postweaning investment in daughters, making it difficult to make reliable comparisons of total maternal costs in each sex (Johnson, 1986; Clutton-Brock et al., 1982; Clutton-Brock, 1991). Second, in the absence of a brother single female offspring can reach maternal feeding rates similar to those obtained by single male offspring. This, as suggested above, supports our conclusion that the factor determining a decrease in maternal feeding rate to female chicks in mixed-sex broods is the competitive interaction with their male siblings.

In sum, our results show that male chicks of mixed-sex broods received more maternal feedings than their sisters, and that this probably causes a female-biased mortality in these broods, a pattern which is opposite to the typical overall male-biased mortality in this species. However, we did not find any evidence of a maternal preference to feed their sons more than their daughters, even in mothers of higher than average condition as those studied here. Future studies (in prep.) will investigate whether great bustards have facultative sex-allocation mechanisms at earlier breeding phases (egg development, laying), but the results presented here on maternal expenditure during the offspring growth phase are more compatible with the differential mortality hypothesis, i.e. the existence of a conflict among siblings caused by a more intensive soliciting behavior of male chicks, due to their markedly higher food requirements consequent with their faster growth rates, which in this species are ultimately determined by a strong sexual selection.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

References

- Alonso JC, Alonso JA. 1990. Parámetros Demográficos, Selección de Hábitat y Distribución de la Avutarda (*Otis tarda*) en Tres Regiones Españolas. Madrid, Spain: ICONA.
- Alonso JC, Alonso JA. 1992. Male-biased dispersal in the Great Bustard (*Otis tarda*). *Ornis Scan.* 23:81-88.
- Alonso JC, Martín E, Alonso JA, Morales MB. 1998. Proximate and ultimate causes of natal dispersal in the great bustard, *Otis tarda*. *Behav Ecol.* 9:243-252.
- Alonso JC, Martín CA, Palacín C, Magaña M, Martín B. 2003. Distribution, size and recent trends of the great bustard *Otis tarda* population in Madrid region, Spain. *Ardeola.* 50(1):21-29.
- Alonso JC, Martín CA, Palacín C, Martín B, Magaña M. 2005a. The Great Bustard *Otis tarda* in Andalusia, southern Spain: status, distribution and trends. *Ardeola.* 52(1):67-78.
- Alonso JC, Palacín C, Martín CA, Mouati N, Arhzaf ZL, Azizi D. 2005b. The Great Bustard *Otis tarda* in Morocco: a re-evaluation of its status based on recent survey results. *Ardeola.* 52(1):79-90.
- Alonso JC, Magaña M, Alonso JA, Palacín C, Martín CA, Martín B. 2009. The most extreme sexual size dimorphism among birds: allometry, selection, and early juvenile development in the great bustard. *Auk.* 126:657-665.
- Alonso JC, Magaña M, Palacín C, Martín CA. 2010. Correlates of male mating success in great bustard leks: the effects of age, weight and display effort. *Behav Ecol Sociobiol.* 64:1589-1600.
- Anderson DJ, Budde C, Apanius V, Gomez JEM, Bird DM, Weathers WW. 1993. Prey size influences female competitive dominance in nestling American kestrels (*Falco sparverius*). *Ecology.* 74:367-376.
- Bortolotti GR. 1986. Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *Am Nat.* 127:495-507.
- Burfening PJ. 1972. Prenatal and postnatal competition among twin lambs. *Anim Prod.* 15:61-66.

709 Cameron EZ. 2004. Facultative adjustment of mammalian sex ratios in support of the
710 Trivers–Willard hypothesis: evidence for a mechanism. *Proc R Soc Lond B*.
711 271:1723–1728.

712 Carranza J. 2002. What did Trivers and Willard really predict? *Anim Behav*. 63:F1–F3.

713 Carranza J. 2004. Sex allocation within broods: the intrabrood sharing-out hypothesis.
714 *Behav Ecol*. 15:223–232.

715 Charnov EL. 1982. *The Theory of Sex Allocation*. Princeton: Princeton University
716 Press.

717 Clutton-Brock TH. 1991. *The evolution of parental care*. Princeton: Princeton
718 University Press.

719 Clutton-Brock TH, Albon SD. 1982. Parental investment in male and female offspring
720 in mammals. In: Kings College Sociobiology Group, editors. *Current problems*
721 *in Sociobiology*. Cambridge: Cambridge University Press. p. 223–247.

722 Clutton-Brock TH, Albon SD, Guinness FE. 1982. *Red Deer: Behavior and Ecology of*
723 *Two Sexes*. Edinburgh: Edinburgh University Press.

724 Clutton-Brock TH, Albon SD, Guinness FE. 1985. Parental investment and sex
725 differences in juvenile mortality in birds and mammals. *Nature*. 313:131–133.

726 Cockburn A, Legge S, Double MC. 2002. Sex ratios in birds and mammals: can the
727 hypotheses be disentangled?. In: Hardy ICW, editor. *Sex Ratios. Concepts and*
728 *Research methods*. Cambridge: Cambridge University Press. p. 266–286.

729 Drummond H. 2001. The control and function of agonism in avian broodmates. *Adv*
730 *Study Behav*. 30:261–301.

731 Drummond H, Gonzalez E, Osorno JL. 1986. Parent-offspring cooperation in the blue-
732 footed booby (*Sula nebouxii*): social roles in infanticidal brood reduction. *Behav*
733 *Ecol Sociobiol*. 19:365–372.

734 Dzus EH, Bortolotti GR, Gerrard JM. 1996. Does sex-biased hatching order in bald
735 eagles vary with food resources? *Ecoscience*. 3:252–258.

736 Fisher RA. 1930. *The genetical theory of natural selection*. Oxford: Oxford University
737 Press.

738 Frank SA. 1987. Individual and population sex allocation patterns. *Theor Popul Biol*.
739 31:47–74.

740 Frank SA. 1990. Sex allocation theory for birds and mammals. *Ann Rev Ecol Syst*.
741 21:13–55.

742 Froy H, Walling CA, Pemberton JM, Clutton-Brock TH, Kruuk LEB. 2016. Relative
743 costs of offspring sex and offspring survival in a polygynous mammal. *Biol Lett.*
744 12:20160417.

745 Godfray HCJ, Werren JH. 1996. Recent development in sex ratio studies. *Trends Ecol*
746 *Evol.* 11:59–63.

747 Gomendio M, Clutton-Brock TH, Albon SD, Guinness FE, Simpson MJA. 1990.
748 Mammalian sex ratios and variation in the cost of rearing sons and daughters.
749 *Nature.* 343:261-263.

750 Hardy ICW. 1997. Possible factors influencing vertebrate sex ratios: and introductory
751 overview. *Appl Anim Behav Sci.* 51:217-241.

752 Hewison AJM, Gaillard JM. 1999. Successful sons or advantaged daughters? The
753 Trivers–Willard model and sex-biased maternal investment in ungulates. *Trends*
754 *Ecol Evol.* 14:229–234.

755 Johnson CN. 1986. Philopatry, reproductive success of females and maternal investment
756 in the red-necked wallaby. *Behav Ecol Sociobiol.* 19:143-150.

757 Kalmbach E, Benito MM. 2007. Sexual size dimorphism and offspring vulnerability in
758 birds. In: Fairbairn DJ, Blanckenhorn WU, Székely T, editors. *Sex, Size and*
759 *Gender Roles: Evolutionary Studies of Sexual Size Dimorphism.* Oxford:
760 Oxford University Press. p. 133-142.

761 Kenward RE. 2001. A manual for wildlife radio tagging. Academic Press, New York

762 Korsten P, Clutton-Brock T, Pilkington JG, Pemberton JM, Kruuk, LEB. 2009. Sexual
763 conflict in twins: male co-twins reduce fitness of female Soay sheep. *Biol Lett.*
764 5: 663-666.

765 Kovacs KM, Lavigne DM. 1986. Growth of grey seal (*Halichoerus giypus*) neonates:
766 differential maternal investment in the sexes. *Can J Zool.* 64:1937-
767 1943.

768 Krackow S. 2002. Why parental sex ratio manipulation is rare in higher
769 vertebrates. *Ethology.* 108:1041-1056.

769 Kretzmann MB, Costa DP, Le Boeuf BJ. 1993. Maternal energy investment in elephant
770 seal pups: evidence for sexual equality? *Am Nat.* 141: 446-480.

771 Labocha MH, Hayes JP. 2012. Morphometric indices of body condition in birds. a
772 review. *J. Ornithol.* 153: 1-22.

773 Lee PC, Moss C J. 1986. Early maternal investment in male and female African
774 elephant calves. *Behav Ecol Sociobiol.* 18:353-361.

775 Leimar O. 1996. Life-history analysis of the Trivers and Willard sex-ratio problem.
 776 Behav Ecol. 7:316-325.
 777 Lessells K. 1998. A theoretical framework for sex-biased parental care. Anim Behav.
 778 56:395–407.
 779 Litzbarski H, Litzbarski B. 1998. Bericht über die Aufzucht und Auswilderung der
 780 Grosstrappen in den Jahren 1979-1997. Naturschutzstation Buckow, Germany.
 781 Unpubl. report.
 782 Litzbarski B, Jaschke M, Jaschke W. 1983. Zur Problematik der Aufzucht und
 783 Auswilderung von Jungtrappen in Buckow. Naturschutzarbeit in Berlin und
 784 Brandenburg. 6:48-54.
 785 Lummaa V, Pettay JE, Russell AF. 2007. Male twins reduce fitness of female co-twins
 786 in humans. P Natl Acad Sci USA. 104:10915–10920.
 787 Magaña M. 2007. Comportamiento reproductivo de la Avutarda Común. PhD thesis,
 788 Madrid: Universidad Complutense.
 789 Martín E. 1997. Dispersión juvenil y cuidado maternal en la Avutarda (*Otis tarda*). PhD
 790 thesis, Madrid: Universidad Autónoma.
 791 Martín CA, Alonso JC, Alonso JA, Palacín C, Magaña M, Martín B. 2007. Sex-biased
 792 juvenile survival in a bird with extreme size dimorphism, the Great Bustard *Otis*
 793 *tarda*. J Avian Biol. 38:335–346.
 794 Medland SE, Loehlin JC, Willemsen G, Hatemi PK, Keller MC, Boomsma DI, Eaves
 795 LJ, Martin NG. 2008. Males do not reduce the fitness of their female co-twins in
 796 contemporary samples. Twin Res Hum Genet. 11:481–487.
 797 Merklings T, Welcker J, Hewison AJM, Hatch SA, Kitaysky AS, Speakman JR, Danchin
 798 E, Blanchard P. 2015. Identifying the selective pressures underlying offspring
 799 sex ratio adjustments: a case study in a wild seabird. Behav Ecol 26:916-925.
 800 Mock DW. 1984. Infanticide, siblicide and avian nestling mortality. In: Hausfater G,
 801 Hrdy SB, editors. Infanticide: comparative and evolutionary perspectives. New
 802 York: Aldine. p. 3-30.
 803 Mock DW. 1985. Siblicidal brood reduction: the prey-size hypothesis. Am Nat.
 804 125:327-343.
 805 Mock DW, Parker GA. 1997. The evolution of sibling rivalry. New York: Oxford
 806 University Press.

807 Mock DW, Lamey TC, Williams CF, Pelletier A . 1987. Flexibility in the development
808 of heron sibling aggression: an intraspecific test of the prey-size hypothesis.
809 Anim Behav. 35:1386-1393.

810 Morales MB, Alonso JC, Alonso JA. 2002. Annual productivity and individual female
811 reproductive success in a great bustard *Otis tarda* population. Ibis. 144:293-300.

812 Nager RG, Monaghan P, Griffiths R, Houston DC, Dawson R. 1999. Experimental
813 demonstration that offspring sex ratio varies with maternal condition. P Natl
814 Acad Sci USA. 96:570-573.

815 Oddie KR. 2000. Size matters: competition between male and female great tit offspring.
816 J Anim Ecol. 69:903-912.

817 Pen I, Weissing FJ. 2002. Optimal sex allocation : steps towards a mechanistic theory.
818 In: Hardy ICW, editor. Sex ratios. Concepts and research methods. Cambridge:
819 Cambridge University Press. p. 26–47.

820 Raberg L, Stjernman M, Nilsson JA. 2005. Sex and environmental sensitivity in blue tit
821 nestlings. Oecologia. 145:496-503.

822 Redondo T, Gomendio M, Medina R. 1992. Sex-biased parent-offspring conflict.
823 Behavior. 123(3-4):261-289.

824 Robert KA, Schwanz LE, Mills HR. 2010. Offspring sex varies with maternal
825 investment ability; empirical demonstration based on cross-fostering. Biol Lett.
826 6:242-245.

827 Sheldon BC. 1998. Recent studies of avian sex ratios. Heredity. 80:397-402.

828 Sheldon BC, West SA. 2004. Maternal dominance, maternal condition, and offspring
829 sex ratio in ungulate mammals. Am Nat. 163:40–54.

830 Stamps JA. 1990. When should avian parents differentially provision sons and
831 daughters? Am Nat. 135:671-685.

832 Stamps J, Clark A, Arrowood P, Kus B . 1985. Parent-offspring conflict in budgerigars.
833 Behavior. 94:1-40.

834 Stamps J, Clark A, Arrowood P, Kus B. 1989. Begging behavior in budgerigars.
835 Ethology. 81:177-192.

836 Trivers RL, Willard DE. 1973. Natural selection of parental ability to vary the sex ratio
837 of offspring. Science. 179:90-91.

838 Uller T. 2006. Sex-specific sibling interactions and offspring fitness in vertebrates:
839 patterns and implications for maternal sex ratios. Biol Rev. 81:207–217.

840 West SA. 2009. Sex allocation. Princeton: Princeton University Press.

841 West SA, Sheldon BC. 2002. Constraints in the evolution of sex ratio adjustment.
842 Science. 295:1685–1688.
843 West SA, Reece SE, Sheldon BC. 2002. Sex ratios. Heredity. 88:117–124.
844 Wilson AJ, Pilkington JG, Pemberton JM, Coltman DW, Overall ADJ, Byrne KA,
845 Kruuk LEB. 2005. Selection on mothers and offspring: whose phenotype is it
846 and does it matter? Evolution. 59:451–463.

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Animal welfare note:

Instaed of an Ethical Note, and following instrucionts for authors, I have included all relevant items that need ethical consideration in methods, in the places requested by reviewer 3.